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Alex K. Baranowski
University of Rhode Island

Steven R. Alm

Evan L. Preisser
University of Rhode Island, preisser@uri.edu

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Alex Baranowski
Department of Biological Sciences
University of Rhode Island
Woodward Hall
9 East Alumni Avenue
Kingston, RI 02881 USA
(860) 378-7430
alexbaran74@gmail.com

Datana drexelii (Lepidoptera: Notododontidae) occurrence and larval survival on highbush blueberry cultivars

ALEX K. BARANOWSKI[1*], STEVEN R. ALM[2], and EVAN L. PREISSER[1]

[1]Department of Biological Sciences, University of Rhode Island, Kingston, RI 02881
[2]Department of Plant Sciences and Entomology, University of Rhode Island, Kingston, RI 02881

Abstract

Plant genotype influences plant suitability to herbivores; domesticated plants selected for properties such as high fruit yield may be particularly vulnerable to herbivory. Cultivated strains of highbush blueberry, *Vaccinium corymbosum* L. can be high-quality hosts for larvae of the gregariously-feeding notodontid *Datana drexelii* (Hy. Edwards). We conducted an experiment assessing *D. drexelii* larval survival and pupal weight when fed foliage from five blueberry cultivars: ‘Bluecrop’, ‘Bluetta’, ‘Blueray’, ‘Lateblue’, and ‘Jersey’. We complemented this experimental work with repeated bush-level surveys of a managed blueberry patch for naturally occurring *D. drexelii* larval clusters. Larval survival and pupal weight were significantly higher on ‘Lateblue’ foliage than from the ‘Bluecrop’, ‘Bluetta’, and ‘Jersey’ cultivars. The blueberry patch surveys found more *D. drexelii* larval clusters on ‘Bluehaven’, ‘Collins’, and ‘Darrow’ bushes than on the cultivars ‘Earliblue’ and ‘Jersey’. The low *D. drexelii* occurrence and performance on the ‘Jersey’ cultivar suggests that this variety may be appropriate for areas where this pest is common; conversely, their high occurrence on ‘Bluehaven’ ‘Collins’, and ‘Darrow’ suggests that these cultivars may be particularly vulnerable. Cultivar-level variation in herbivore vulnerability highlights how understanding plant-pest interactions can help manage agricultural species.

Keywords

Herbivory, preference, performance, defoliator

Introduction

Herbivore fitness is influenced by host plant phenotype. Although wild plants experience strong selection for herbivore tolerance and/or resistance, domesticated plants are subjected to different pressures. Selection for high fruit yield in domesticated plants, for example, can reduce plant defense against herbivores (Sanchez-Hernandez et al. 2006, Turcotte et al. 2014, Hernandez-Cumplido et al. 2018). Larvae of *Lymantria dispar* L. (Lepidoptera: Erebidae) grow more quickly and have lower mortality when reared on domesticated versus wild-type *Vaccinium corymbosum* L. (Hernandez-Cumplido et al. 2018). Wild-type tomatoes (*Solanum lycopersicum* L.) produce more phenolic compounds than domesticated ones (Sanchez-Hernandez et al. 2006), and growth rate of the moth *Manduca sexta* L. (Lepidoptera: Sphingidae) is negatively correlated with such phenolics (Stamp and Yang 1996, Yang and Stamp 1996).

Vaccinium corymbosum (hereafter 'blueberry') is a deciduous ericaceous plant native to North America grown commercially for its fruits. As with other agricultural plants, blueberry has multiple cultivars that have been selected for yield, flavor, or pest/disease resistance (Lobos and Hancock 2015, Clift et al. 2017, Rodriguez-Saona et al. 2019). Cultivar-related differences in herbivore growth and mortality have been recorded in lepidopteran species such as *Streblote panda* (Hübner, 1820) (Lepidoptera: Lasiocampidae) (Calvo and Molina 2010), and tephritid flies such as *Bactrocera dorsalis* (Hendel), *Ceratitis capitata* (Wiedemann, 1824) (Follett et al. 2011) and *Rhagoletis mendax* (Curran) (Liburd et al. 1998).

Members of the notodontid genus *Datana* (Walker, 1855) are defoliating pests of agricultural, silvicultural, and horticultural crops (Cutler and Harris 1979, Harris 1983). *Datana drexelii* (Hy. Edwards) (hereafter '*Datana*') is a native defoliating pest of ericaceous plants in the genera *Vaccinium* L. and *Gaylussacia* (Kunth). Females lay clusters of up to 200 eggs on suitable host plants; their gregarious nature, combined with the fact that larvae can reach six cm in length, make it an especially destructive pest (Wagner 2005). While this insect does not directly attack fruit, its defoliation of blueberry bushes reduces the following year's flowering and subsequent fruit crop (Lyrene 1992, Williamson and Miller 2000). We reared *Datana* larvae on different blueberry cultivars and measured their survival to pupation and pupal weight. In addition, we repeatedly surveyed a patch planted with multiple blueberry cultivars for naturally-occurring clusters of *Datana* larvae. Together, the data reveal substantial differences in *Datana* preference for and occurrence on different blueberry cultivars.

Materials and Methods

Performance Assay: In June 2019, we mated adults from a lab colony of *Datana drexelii,* reared on wild-type *V. corymbosum*, in an outdoor emergence cage at the University of Rhode Island's East Farm research facility (Kingston, RI). We collected their eggs and assigned five each to 946 mL polypropylene cups (Pactiv LLC, Lake Forest, IL). Each cup was randomly assigned to one of five blueberry cultivars: 'Bluecrop', 'Blueray', 'Bluetta', 'Jersey', or 'Lateblue'. There were 22-23 replicate cups per cultivar. Eggs in a given cup generally hatched on the same day; in three cups one day, and in one cup two days, elapsed between the emergence of the first and last hatchling. Host foliage from the appropriate cultivar was added to the cup immediately following emergence of the first hatchling. Larvae received four-leaf sections of foliage from current year's growth (as indicated by soft, green bark); no other leaf position standardization was done. Prior to adding foliage to each container, each piece was dipped in a 2% bleach (=0.1% NaOCl) solution and allowed to air dry; this measure was taken to decrease the threat posed by pathogenic fungi and bacteria (Trivedy et al. 2011). Foliage was replaced every three days or as needed to ensure a constant food supply.

Four days after the last hatchling in a given cup eclosed, we weighed all hatchlings together and counted the number of larvae and unhatched eggs. The total number of hatched larvae was our starting number of larvae for a cup, regardless of how many eggs hatched. We used this data to calculate post-hatching survival. Larvae were subsequently counted and weighed together each week; we recorded the date each larva entered the prepupal phase. Prepupae were left in cups until all larvae in a cup reached such a state or died. When all prepupae had either died or become pupae, each pupa was sexed, weighed and then held in a 6L polypropylene bin (Sterilite Corp, Townsend, MA) of moist coconut coir for overwintering.

Occurrence Assay: In summer 2019, we conducted a six-week *Datana* survey of an East Farm blueberry patch enclosed in bird-proof netting that did not exclude insects. The patch consisted of 240 bushes arranged in eight rows of 30 bushes. The cultivars represented (numbers of bushes in parentheses) were 'Bluecrop' (25), 'Bluegold' (5), 'Bluehaven' (15), 'Bluejay' (15), 'Blueray' (15), 'Bluetta' (15), 'Chandler' (5) 'Collins' (20), 'Darrow' (20), 'Earliblue' (30), 'Herbert' (15), 'Jersey' (15), 'Lateblue' (15), 'Northland' (15), and 'Reka' (15). Cultivars were arranged in five-bush groups within a given row.

Between July 16th and August 26th, we conducted 15 total censuses (with as many as nine days and as few as one day between censuses) for *Datana* larval clusters. We walked on both sides of each bush and scanned for larval clusters. We spent a minimum of thirty seconds per bush and longer if necessary and recorded the number of larval clusters on each bush before removing them from the bush. Following the final census, we measured the height and maximum width of each bush.

Statistical Analysis: For the performance assay, mean pupal weight and percent survival (average per cup) to pupation were analyzed using analysis of covariance (ANCOVA), with 'cultivar' as the main effect and 'hatch date' and, because we were concerned about sex-mediated performance differences, 'number of female pupae per cup' as covariates. We excluded 15 cups in which only a single larva hatched, leaving a total of 98 cups (=replicates). When the ANCOVA revealed a significant main effect, we used Tukey's HSD tests (α=0.05) to differentiate between treatment. We also conducted an overall linear correlation analysis between weight and survival across all cultivars.

For the occurrence assay, we summed the total number of larval clusters counted per bush over the fifteen censuses. Prior to analysis, we removed data from two cultivars, 'Bluegold' and 'Chandler', only represented by a single five-bush cluster within the patch; all other cultivars were each represented by between three and six five-bush clusters. During our surveys, we noticed that small (~0.5 m in height) recently-planted bushes had virtually no larval clusters regardless of their cultivar. We addressed this bias by excluding bushes below the 10th percentile in height (0.7 m) from the analysis; this excluded 27 bushes from five cultivars but only two of 108 larval clusters. We used GLMM (poisson distribution with log-link function) to analyze the 203-bush data set. The model was generated with the main effect 'cultivar' and the blocking variables 'row' and 'column' as random effects; 'bush height' was included as a covariate. The GLMM was initially run using both blocking variables; the non-significant blocking variable 'row' was then removed and the resulting GLMM re-run. When the GLMM revealed a significant main effect of 'cultivar', we used likelihood-ratio χ-square tests (α=0.05; controlled for type 1 errors due to multiple comparisons) to differentiate between treatments.

All analyses were performed using JMP 9.0.0 (SAS 2010).

Results

Performance Assay: Larvae reared on ‘Lateblue’ pupated at nearly three times the weight of larvae reared on ‘Blueray’, ‘Bluetta’, and ‘Jersey’ (0.375 g versus 0.127 g, respectively; $F_{4,91} = 3.18$, $P = 0.017$; Fig. 1A). Survival to pupation was also higher on ‘Lateblue’ than on ‘Bluecrop’, ‘Bluetta’, and ‘Jersey’ (16.9% versus 5.1%; $F_{4,91} = 3.62$, $P = 0.009$; Fig. 1B). Hatch date affected survival, with later-hatching larvae having higher mortality ($F_{1,91} = 7.84$, $P = 0.006$). The number of female pupae per cup was correlated with both weight at and survival to pupation (both $P < 0.001$). There was a significant cultivar-level correlation between mean pupal weight and mean survival to pupation ($R^2 = 0.84$, $F_{1,3} = 15.6$, $P = 0.029$).

Occurrence Assay: We found a total of 108 *Datana* larval clusters over the six-week course of the survey. The distribution of larval clusters over time was as follows: 14 on July 16th, ten on July 18th, 35 on July 22nd, one on July 23rd, five on July 25th, three on July 26th, one on July 29th, two on July 30th, two on July 31st, 11 on Aug. 1st, 12 on Aug. 2nd, one on Aug. 6th, two on Aug. 11th, eight on Aug. 20th, and one on Aug. 26th. Cultivars differed in *Datana* colonization (L-R $\chi^2 = 28.01$ with 12 df, p = 0.006; Fig. 2), with ‘Bluehaven’, ‘Collins’, and ‘Darrow’ having more *Datana* clusters (1.00/bush, 0.75/bush, and 0.85/bush, respectively) than either ‘Jersey’ or ‘Earliblue’ (0.13 and 0.07 per bush, respectively). Neither bush height (L-R $\chi^2 = 0.52$ with 1 df, p = 0.47) nor column (L-R $\chi^2 = 39.3$ with 29 df, p = 0.096) affected *Datana* colonization.

Discussion

Datana larval performance in the lab did not overlap with field observations. Despite high larval performance on ‘Lateblue’, larval occurrence on it was not the highest on this cultivar in the field survey. High *Datana* densities on ‘Bluehaven’, ‘Collins’, and ‘Darrow’, cultivars not included in our performance assay, suggest they may be particularly suitable to this pest. In contrast, both occurrence and performance were significantly lower for ‘Earliblue’ and ‘Jersey’ than other tested cultivars (Figs. 1, 2). This implies that ‘Earliblue’ and ‘Jersey’ may have antixenotic and antibiotic effects on *Datana*.

Mortality in the performance assay occurred mostly within a week of hatching, when larvae were small and inconspicuous. Our high early larval mortality across treatments could indicate that either cultivated blueberry is unsuitable for this species (comparison to wild-type blueberry is needed to determine this), or perhaps that the unnaturally low early instar densities could be reducing the feeding ability, and thus survival, of hatchlings (Dave Wagner, pers. comm). It is also possible that the quality of the cut blueberry may diminish more quickly than the foliage is replaced (within 24hrs instead of 3 days), malnourishing larvae. If similarly high levels of hatchling mortality also occurred in the field survey, we could have missed some oviposition events when all larvae died prior to reaching a detectable size. Because of this, the patterns in our field survey data likely reflect some combination of female oviposition preference and plant resistance to early-instar larval feeding. While most larval clusters contained a similar number (10-20 individuals) of small 2nd-3rd instar larvae, we failed to detect some clusters until they contained 4th-5th instar larvae. The laboratory-based oviposition choice tests necessary to isolate the role of female preference may be complicated by this species’ habit of readily ovipositing on container walls and other artificial objects.

Our work could be extended to comparisons of *Datana* interactions with cultivated versus wild-type blueberry, as well as with other *Vaccinium* species. Selective breeding for pest resistance (Lobos and Hancock 2015) and the incorporation of several related *Vaccinium* species into *V. corymbosum* cultivars (Lobos and Hancock 2015) may alter the cultivar’s suitability to *Datana*. Both ‘Lateblue’ and ‘Jersey’, cultivars on which larvae did the best and worst, are pure *V. corymbosum*, but ‘Bluecrop’ is 4% *Vaccinium angustifolium* (Aiton, 1789) and ‘Bluetta’ is

28% *V. angustifolium*. Some cultivars are only 42% *V. corymbosum* and contain genes from up to five other species (Lobos and Hancock 2015). Intrageneric variation in herbivore susceptibility has been described for other *Vaccinium* (Ieri et al. 2013) species as well as for genera ranging from *Asclepias* L. (Waterbury et al. 2019) to *Quercus* L. (Rieske and Dillaway 2008).

In summary, there were blueberry cultivar-related differences in occurrence and performance of this blueberry defoliator. This information could prove useful for cultivar selection in areas where this pest becomes a major problem, and highlights how understanding plant-pest interactions can help reduce the need for costly chemical or mechanical (removal of individual larval clusters) treatments.

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Figure Legends

Figure 1. Mean (± SE) *Datana drexelii* pupal weight (A) and mean (± SE) *D. drexelii* survival to pupation (B) when reared on five different *Vaccinium corymbosum* cultivars. Bars with different uppercase letters are significantly different (Tukey's HSD at $\alpha = 0.05$).

Figure 2. Mean ± (SE) *D. drexelii* larval clusters counted per bush for 13 *V. corymbosum* cultivars over the course of six weeks and fifteen censuses. Cultivars in dark blue were included in the performance assay (Fig. 1). Bars with different uppercase letters are significantly different (Tukey's HSD at $\alpha = 0.05$).

246 Figure 1.

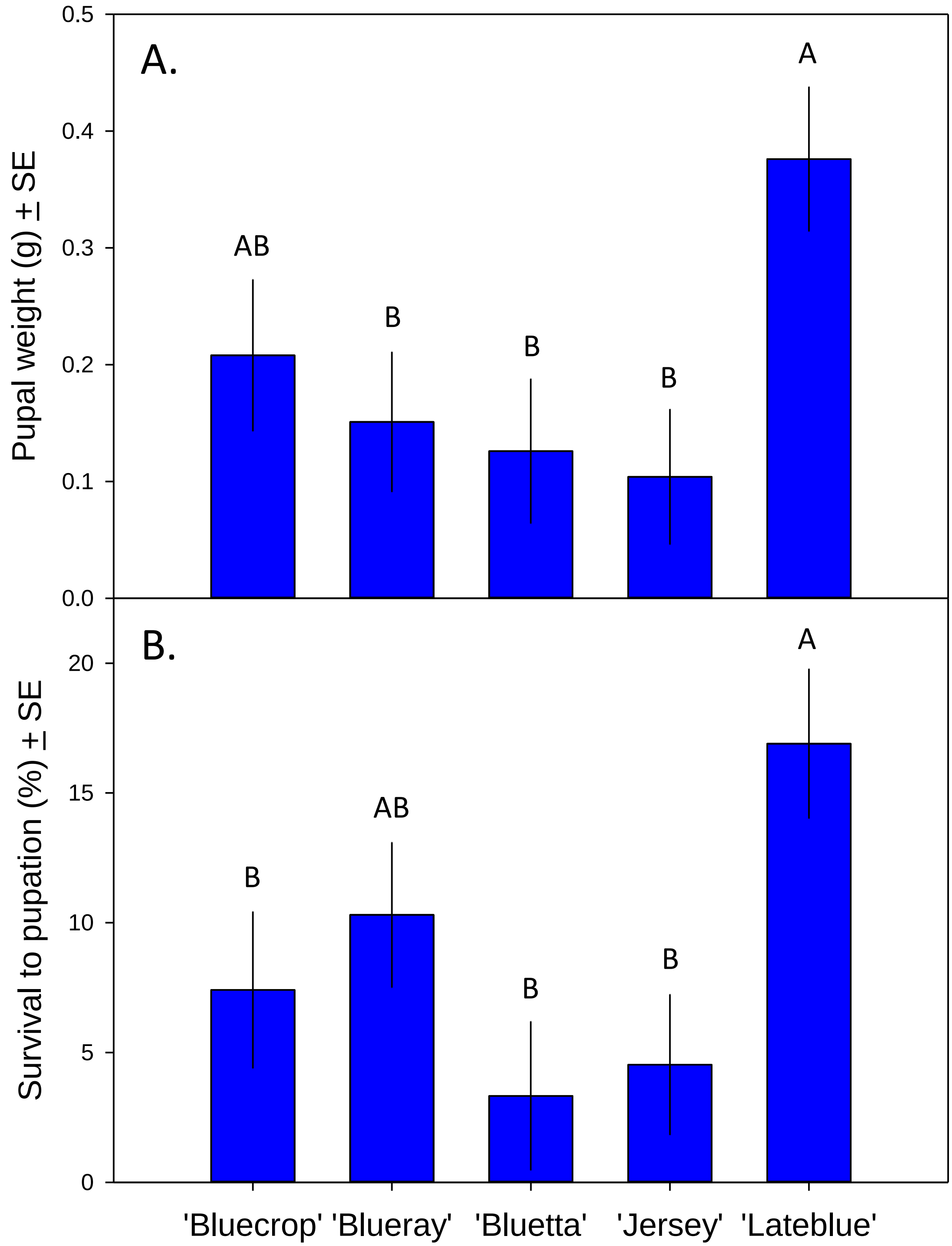
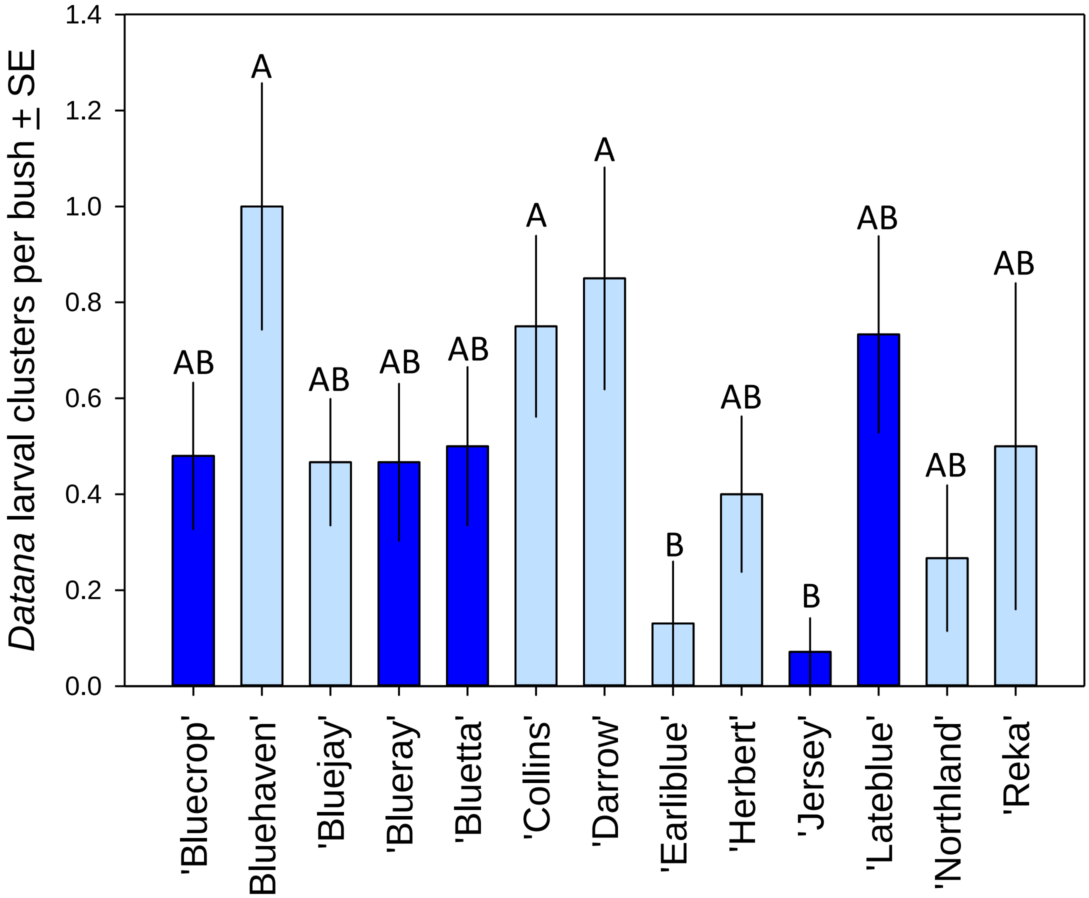

0.5
A.
A
0.4
Pupal weight (g) ± SE
0.3
AB
B
0.2
B
B
0.1
0.0
B.
20
A
Survival to pupation (%) ± SE
15
AB
B
10
B
B
5
0
'Bluecrop' 'Blueray' 'Bluetta' 'Jersey' 'Lateblue'

Figure 2.


Datana larval clusters per bush ± SE
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
AB
A
AB
AB
AB
A
A
B
AB
B
AB
AB
AB
'Bluecrop'
'Bluehaven'
'Bluejay'
'Blueray'
'Bluetta'
'Collins'
'Darrow'
'Earliblue'
'Herbert'
'Jersey'
'Lateblue'
'Northland'
'Reka'